Genetic similarity promotes evolution of cooperation under lethal intergroup competition

Oleg Smirnov[1] & John Orbell[2]

[1]*Department of Political Science, Stony Brook University, Stony Brook, NY 11794, USA*

[2]*Institute of Cognitive and Decision Sciences, University of Oregon, Eugene OR 97403, USA*

Altruism (helping others at a cost to oneself) may evolve via group selection if the cost of altruism to the individual is compensated for by growth differences among groups when (1) there is high genetic variation among members of different groups; (2) more altruistic groups grow faster and (3) between-group migration is low. Nevertheless, group selection may not fully explain the actual evolution of helping behaviour if between-group migration was sufficiently common to have reduced between-group genetic variance. Lethal intergroup competition, which amplifies such growth differences between groups, appears to have been frequent in humans' ancestral environments and could bear importantly on the evolution of altruism. Here we show that between-group migration and resulting genetic similarity can *promote* the evolution of costly helping behavior in the context of lethal intergroup conflict, albeit by selection at the individual level and not by group selection. The standard group selection models do not capture such basic elements of lethal intergroup competition as the possibility of an individual's altruism being critical to the group's success when that possibility is *inversely* proportional to genetic variation among members of the competing groups.

Lethal intergroup competition appears to have been frequent in humans' ancestral environments[1,2] and increasing scholarly recognition[3] that such competition could bear importantly on the evolution of altruism is valuable. Whether by individual or multilevel selection[4-6], altruism can evolve if and only if it advances the altruist's reproductive success[7-9]. Warfare certainly can have implications for an individual's success, both as a consequence of what happens at the group level (victory or defeat) and of consequences for the individual, whether cooperator or free-rider. If altruists' reproductive gains from war-related events at the group level are greater than their personal losses from war-related altruism, then the latter attribute can evolve[10,11]. The standard model of group selection[3] suggests that this is most likely when groups are broadly *different* in altruism as derived from the Price equation[10,11]. The feasibility of that model depends critically on the answer to the following empirical question: Were genetic differences between early human groups great enough to allow for the evolution of altruism via group selection?

One implication of the group selection model of lethal intergroup competition[3] is that paying a cost to help one's group survive in lethal intergroup competition may provide direct reproductive benefits for an individual and, therefore, that a trait supporting such altruism can evolve without group selection. The expected benefit from cooperation is greatest when: (a) group extinction rates are high, (b) contending groups are small, (c) cooperation differences are important for the probability of group survival, and (d) when the contest is competitive, viz., when the genetic difference between the groups is small. Evolution of a trait can, of course, only happen in the context of variation on that trait, and that requirement has been developed in standard models of group selection. In the case of lethal conflict among human groups, however, it seems that selection favours cooperation when *between-group* variation on that trait is small.

In a group selection model, the population consists of two types of individuals: cooperators and defectors (see the Methods section for technical details of the model and analysis). Cooperators pay a cost and provide a benefit for the group while defectors free-ride. The population of cooperators and defectors consists of several subpopulations, or demes, competing with each other at the group level. Any two demes have a positive probability of a contest between them. In the event of such a conflict members of one group survive while members of the other group die out. The probability of individual survival, defined as λ, depends on the proportions of cooperators and defectors in two groups, deme size, and an exogenous parameter μ, which is inversely proportional to the "influence of altruists on deme survival"[3]; (Methods). Identical probability of deme survival can be found in the Bowles model[3]. Figure 1 provides an intuitive illustration of λ for three cases of μ.

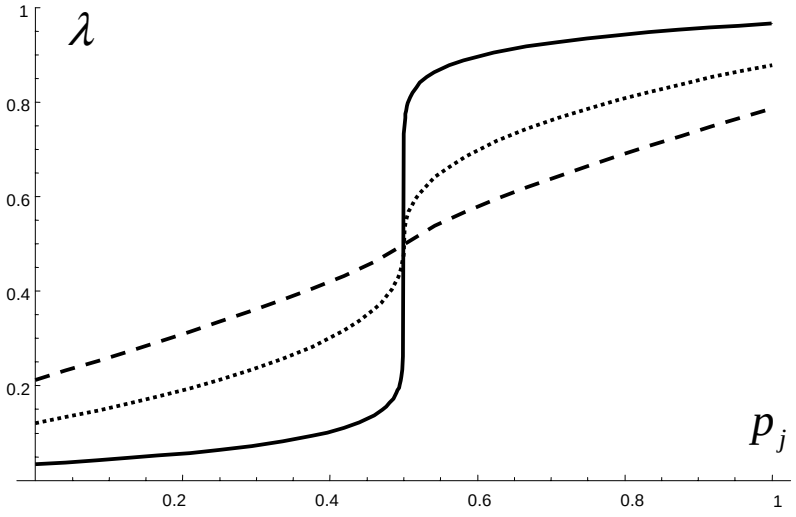

Figure 1 | Probability of survival λ of members of deme j for three cases: $\mu = 0.1$ (solid), $\mu = 0.4$ (dots), $\mu = 0.8$ (dashes). The horizontal axis p_j represents a proportion of cooperators in deme j. The proportion of cooperators in the other deme is assumed to be $p_q = 0.5$. The two demes are further assumed to be of equal size. For small μ, cooperators have the greatest effect on deme survival when the groups are genetically similar, $p_j \approx p_q$.

An individual's switching from defection to cooperation has two effects on that individual's fitness--the private cost of cooperation and the increase in the deme's probability of survival resulting from that cooperative act. The net effect of switching from defection to cooperation, defined as ΔF , is positive when the fitness benefit from increased deme survival is greater than the cost of cooperation. In this case, genetic variation will favour cooperation. Figure 2 shows ΔF for the familiar three cases of μ .

Selection favours cooperation when μ is small and when the groups are genetically similar, i.e., an individual's switching from defection to cooperation has the greatest effect on the probability of his or her deme's survival. Thus, the *smaller* is the genetic difference between competing groups, the *greater* is selection on cooperation. This result is opposite to standard models of the evolution of cooperation via group selection in which the evolutionary success of cooperation is based upon growth differences.

The intuition behind this result is simple. If groups are substantially different genetically—that is, if they have different fractions of cooperators—then the stronger group is very likely to survive and the weaker group is very likely to die out. Then an individual's privately costly cooperative behaviour in either group will be unlikely to affect the outcome and selection will favour selfishness—which, in the long run, would support between-group leveling in the incidence of cooperation. Once groups become genetically similar, selection will favour the cooperative trait since the behaviour associated with that trait will be more likely to affect the probability of one's deme surviving, thus of individuals carrying that trait surviving. The effect of μ is also intuitive since μ is inversely proportional to the "influence of altruists on deme survival"[3]; as $\mu \to 1$ such influence becomes very small and ΔF becomes negative.

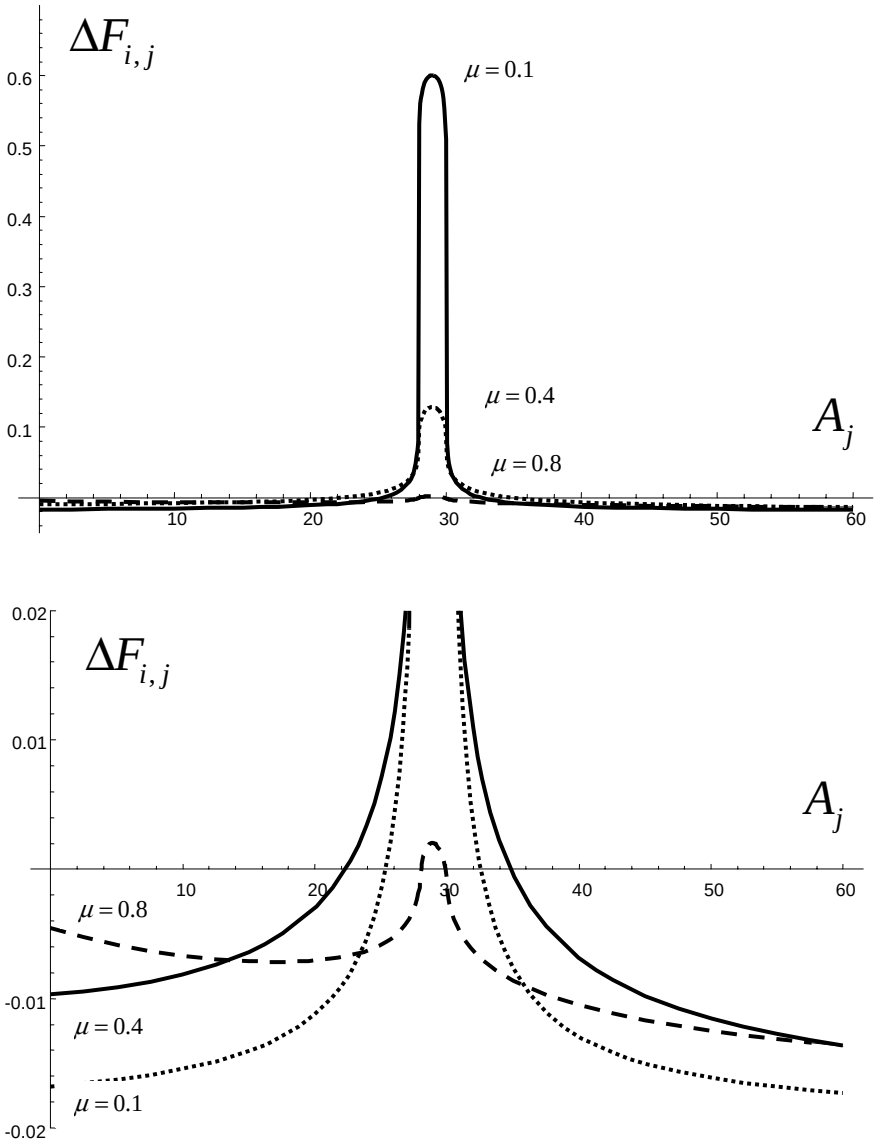

Figure 2 | Fitness benefit from cooperation of an individual i in deme j, $\Delta F_{i,j}$. The horizontal axis A_j is the total number of cooperators in deme j. For the figure, the total number of cooperators in the other deme $A_q = 30$. The three cases of $\Delta F_{i,j}$ are for $\mu = 0.1$ (solid), $\mu = 0.4$ (dots), $\mu = 0.8$ (dashes). The lower graph is a snapshot for $\Delta F_{i,j} \in [-0.02, 0.02]$. Other parameters used: benefit of survival $W = 1$, probability of a conflict $\kappa = 1$, cost of cooperation $c = 0.02$, total number of defectors in both demes $N_j = N_q = 30$. Selection favours cooperation for $\Delta F_{i,j} > 0$ which is the case when the fractions of cooperators in two groups are similar.

Note that the cases of being certain to win and being certain to lose are not exactly symmetric since cooperation appears to provide a greater reproductive benefit when the individual is in a losing group, as opposed to being in a winning group—despite the fact that in both cases an individual is unlikely to have an influence on the probability of his deme's survival.

As Bowles[3] points out, migration among groups is often said to have been frequent enough in the ancestral past to have reduced between-group differences beyond the point at which selective group extinction could offset within-group pressures against altruism. In response, he points to the extraordinarily lethal character of human intergroup competition which could well have made selective group extinction a quite frequent event[1,2], thus increasing the impact of between-group competition. To the contrary, at the individual level, such between-group migration and the consequent reduction of between-group genetic differences would promote selection on the cooperative trait. If empirical evidence were to show only slight genetic differences between groups, cooperation would still evolve in the context of lethal group conflict, absent group selection.

As classically captured by the Price equation, altruism can be selected via between-group differences insofar as more altruistic groups grow faster. Lethal intergroup competition also makes extinction of the whole group possible, meaning that costly cooperation can evolve if such behaviour has an "influence on deme survival"[3], which is more likely when the contending groups are genetically similar. The model proposed here does "take the altruism out of altruism"[12] since selection on cooperation depends on the cooperator's contribution rebounding to personal advantage. Notice, however, that our result does emerge within the standard theoretical framework and is consistent with Bowles' model. In the case of lethal intergroup competition, a

willingness to cooperate for the sake of one's group can evolve without group selection via its direct survival benefits to the individual.

Methods

Consider a metapopulation of two types: cooperators (A's) paying a cost $c > 0$ and defectors, or egoists, (N's) paying nothing. The metapopulation consists of several subpopulations, or demes, competing with each other at the group level. Two demes j and q have an exogenous probability of a contest between them equal to κ. In the event of such a conflict, the expected probability that group j survives this contest is

$$\lambda = 0.5\left\{1+\max\left(p_j - p_q, 0\right)^{\mu} - \max\left(p_q - p_j, 0\right)^{\mu}\right\} \quad (1)$$

where $\mu \in [0,1]$, and p_j and p_q are the fractions of deme j's and deme q's membership that are cooperators. If A_j and A_q are the total numbers of cooperators in groups j and q, and N_j and N_q are the total numbers of defectors, then $p_j = A_j / \left(A_j + N_j\right)$ and $p_q = A_q / \left(A_q + N_q\right)$. The probability of survival λ is, in fact, identical to the one used in the Bowles' model[3] (supplemental materials, expression S13). See Figure 1 for an intuitive illustration of λ for three cases: $\mu = 0.1$, $\mu = 0.4$, and $\mu = 0.8$.

Notice that if an individual in deme j switches from defection to cooperation then p_j becomes equal to $p_j^{'} = \left(A_j + 1\right) / \left(A_j + 1 + N_j - 1\right)$. Consequently, $\Delta p_j = p_j^{'} - p_j$ is the individual's contribution to the increase in the probability of deme j surviving the contest. Assume that each member of the surviving group obtains fitness benefit $W > 0$. Thus, the fitness of an individual i who belongs to group j can be described as

$$F_{i,j} = -ca_{i,j} + \kappa\lambda W \Leftrightarrow \quad (2)$$

$$F_{i,j} = -ca_{i,j} + 0.5\kappa W\left(1+\max\left(\frac{A_j + a_{i,j}}{A_j + N_j} - \frac{A_q}{A_q + N_q}, 0\right)^{\mu} - \max\left(\frac{A_q}{A_q + N_q} - \frac{A_j + a_{i,j}}{A_j + N_j}, 0\right)^{\mu}\right)$$

where $a_{i,j} = 0$ if the individual is a defector, and $a_{i,j} = 1$ if the individual is a cooperator. Cooperators pay the individual cost c but increase the whole group's probability of survival. In the paper, we examine $\Delta F_{i,j} = F_{i,j}\left(a_{i,j} = 1\right) - F_{i,j}\left(a_{i,j} = 0\right)$ which is the net fitness benefit from cooperation. For positive values of $\Delta F_{i,j}$, genetic variation will favour cooperation and for negative values, defection.

1. Keeley, L. H. *War Before Civilization* (Oxford Univ. Press, 1997).

2. LeBlanc, S. & Register K. E. *Constant Battles* (St Martin's Press, 2003).

3. Bowles, S. Group Competition, Reproductive Leveling, and the Evolution of Human Altruism. *Science* 314, 1569-1572 (2006).

4. Traulsen, A. & Nowak, M. A. Evolution of cooperation by multi-level selection. *Proc. Natl. Acad. Sci. U.S.A.* 103, 10952-10955 (2006).

5. Wilson D. S. & Sober E. *Unto Others* (Harvard Univ. Press, 1998).

6. Henrich J. Cultural group selection, coevolutionary processes and large-scale cooperation. *J. Econ. Behav. Organ.* 53, 3-35 (2004).

7. Lehmann L., Keller L., West S., & Roze D. Group selection and kin selection: Two concepts but one process. *Proc. Natl. Acad. Sci. U.S.A.* 104, 6736-6739 (2007).

8. Wilson, E. O. *Sociobiology* (Harvard Univ. Press, 1976).

9. Williams, G. C. *Natural Selection* (Oxford Univ. Press, 1992).

10. Price, G. R. Fisher's 'fundamental theorem' made clear. *Ann. Hum. Genet*. 36, 129-140 (1972).

11. Price, G. R. Selection and covariance. *Nature* 227, 520-521 (1970).

12. Trivers, R. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35-57 (1971).

Author Information The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to O.S. (oleg.smirnov@stonybrook.edu).